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A STUDY OF

A CONTINUOUSLY BREEDING POPULATION OF DANAUS PLEXIPPUS

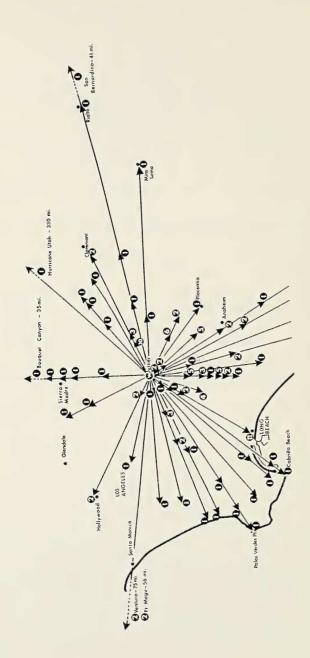
IN SOUTHERN CALIFORNIA COMPARED TO A MIGRATORY POPULATION AND ITS SIGNIFICANCE IN THE STUDY OF INSECT MOVEMENT.

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INTRODUCTION

EARLY IN OUR STUDIES of the movements of the monarch butterfly, it was considered that this species in North America formed a single, gene-flow population the members of which migrated from north to south in the late summer and fall returning the following spring — thus representing a movement similar in many respects to that of a species of migratory bird (Urquhart 1960). However, it was found that in certain parts of North America there were apparently populations that continued to breed throughout the entire year, as in southern California and Florida, or throughout the winter months, as in southwestern Arizona (Funk 1968). Whether the latter population breeds throughout the summer months as well is not indicated. It had also been noted that it is possible to keep breeding populations throughout the year under laboratory conditions (Urguhart & Stegner 1966). It was further observed that females of a migrating population, or those found on over-wintering roosting sites, such as the one located in the Monterey Peninsula of California, failed to oviposit when brought into the laboratory, whereas gravid females collected in the field in the summer and fall laid eggs that gave rise to successive generations (Urquhart & Stegner op. cit.). This has made it possible to have a continuous population for our laboratory experiments on various aspects of insect physiology.



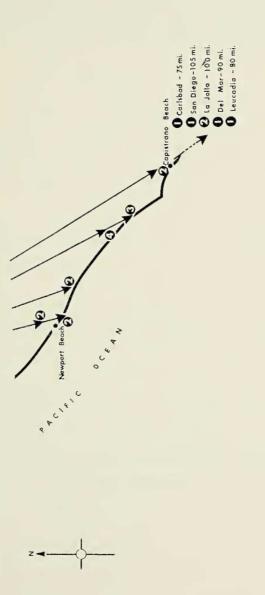


Fig. 1: Flight lines of the movements of monarch butterflies from the release point at Whittier, California. Explanation in text.

As a result of these considerations, and in conjunction with our world-wide studies of the migratory habits of D. plexippus and with particular reference to the eastern North American population (Gulf Coast Population, Urquhart 1966) a study of the movements of the population in southern California (release point at Whittier) was commenced in 1964.

METHOD

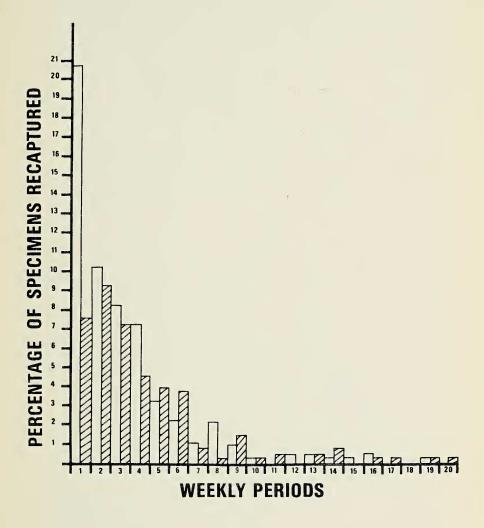
Of the specimens constituting the population studied, most were reared under natural conditions but some were reared under conditions of artificial light and temperature. A preliminary study of the data for these two populations indicated no significant difference in their flight behaviour and therefore the two populations are considered as a single population reared and released in Whittier and southern California.

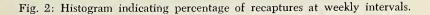
On reaching the imago stage, the specimens were tagged, using the marginal alar tag method, and released. The time and place of the release of each specimen were recorded. Data concerning direction and duration of flight were obtained from recaptured specimens that were mailed to our laboratory at the University of Toronto. All data was recorded and all letters of correspondence concerning each recapture were kept on file for future reference. Preliminary maps and flight charts were constructed so as to indicate whether or not movements were taking place and whether or not they were significant.

PRESENTATION OF RESULTS

A total of 8816 imagoes of both sexes were tagged and released and of these 401 representing both sexes were recaptured and sent to us. The present study is based on the data from these recaptured individuals.

Recapture of specimens that had flown more than one mile from the point of release, and hence indicate a significant movement, were plotted on the map of Los Angeles and Vicinity (fig. 1). Each release-recovery line represents the flight of one or more butterflies. The "v" mark indicates the place where the specimen was recaptured and the number beside the mark shows how many specimens were recaptured at that particular point. The flights of specimens which were on the same flight path were joined together in order to show more clearly the movement of the population in a particular direction. Names of places have been included in order to orient the flight patterns and





hence such place names do not necessarily indicate a particular point of recapture. Long flights that extended beyond the area of the map are indicated on the margin with a notation giving the distance from Whittier to the particular place indicated.

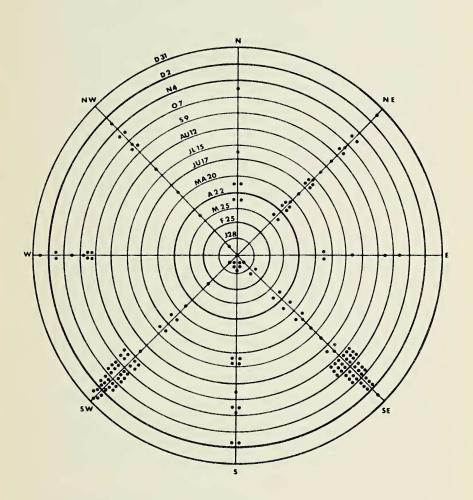
The specimens were released in a well-populated area of Metropolitan Los Angeles which made it possible to obtain a high percentage of recaptures -4.5% as compared to the usual 2% — from all compass points. If releases had been made in a rural district, then areas of no recaptures would have occurred owing to the absence of humans and not necessarily an absence of flights in these particular directions.

An examination of the flight pattern (fig. 1) indicates that there are relatively few flight lines in the sector extending from northeast to west and that the majority of flight lines are to the southwest, south and southeast with the longest flight lines to the south-southeast. There is a conspicuous lack of flight lines in the sector southeast to east, with the exception of a few short flights to the southeast. The absence of long flight lines in this direction might be due to the presence of the Chino Hills and the Santa Ana Mountains deflecting the line of flight, or the sparse human population in this area, or a combination of both factors.

The histogram (fig. 2) shows the time period, in weeks, of recaptures. As one would expect, when a number of specimens are marked and released at a particular geographical locality, there would be more recaptures in the area of release than remote from it. It will be noted that a high proportion (20.8%) of recaptures were made during the first week and had flown less than one mile. A much smaller number (7.6%) traveled more than one mile before being recaptured during the first week.

There is a marked drop in the number of recaptures during the second week, as a result of the thinning out of the population away from the point of release. This is followed by a more gradual decrease in recaptures which finally becomes stabilized after the ninth week.

In the fifth and sixth week more specimens are recaptured after flying more than a mile as compared to those that had flown less than a mile. A similar situation occurs at week nine and week fourteen. This indicates that more individuals of the population had moved away from the point of release than had remained. There is a marked decrease in the number of specimens recaptured after the tenth week reaching a more constant level as the tagged population became more thinly spread out over the countyrside and entered those areas of less dense human population.



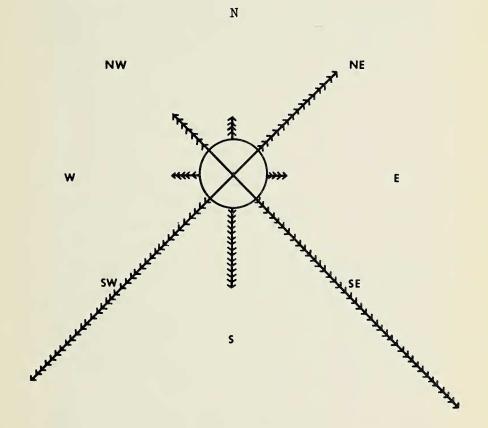


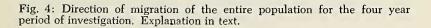
Thus it would appear from the data here presented that within this population some individuals tend to be resident (58%) while others tend to migrate (42%). The proportion of resident individuals might be considerably less than here indicated, however, because as a result of a dense population of tagged specimens located at the point of release, more of them would be recaptured before being able to move out. If, for example, some method could have been employed so that no specimens were recaptured for an arbitrary period of say two weeks, then there would be a greater chance for tagged specimens to move out of the congested area thus decreasing the percentage of what appears to be resident specimens. Of the total number recaptured, 75.5% were recaptured by the end of four weeks and 89.8% by the end of eight weeks while only 6.8% were recaptured between the end of the eighth week and the end of the 20th week. This can be correlated with the decrease in density as the tagged specimens spread out over the countryside away from the point of release.

Fig. 3 presents a graphic analysis of movements of individuals of the population to compass direction at various times of the year. Each concentric line represents intervals of four weeks, commencing at January 1 at the center point. Thus, the first concentric ring represents January 28; the second ring, February 25; and so on. For ease of reference, the month periods have been indicated. The direction of flight is given to eight points of the compass and each recaptured specimen is represented by a dot. Specimens recaptured at the point of release have not been included in the chart.

It will be noted that there is a strong southerly movement between September 9 and December 2. Although movement tends to be random between January 1 and September 9, there is a marked tendency for a northeast flow between March 25 and July 15. Very little directional movement is indicated between July 15 and September 9.

If we examine the movement for the entire population, with the exception of those recaptured at the point of release, and using the method of Williams (1930), in which each arrow point represents a recaptured specimen it becomes obvious that there is a very definite movement away from the point of release towards the southeast and the southwest (fig. 4). There is also a definite tendency of flights to the northeast.





CONCLUSIONS

It would appear, as a result of this study and previous ones, that the monarch butterfly exhibits two types of movement; one extending over long distances as is the case for the Eastern North American Population (Urquhart op. cit.) and others in which the movement is restricted to shorter distances.

Of those that migrate over long distances, as from the eastern parts of the United States and eastern Canada to southern Mexico with a partial return migration, the females enter a period during which no eggs are produced by the ovaries - an ovarian dormancy (Urquhart op. cit.). During the autumnal flight southward such long-distance migrants collect on overnight roosting sites. On certain over-wintering sites, such as occur in the Monterey Peninsula of California, they remain throughout the winter months, (December to February) with no indication of ovarian activity (Urguhart op. cit.). Under laboratory conditions such females taken from the over-night roosting sites or from the over-wintering roosting sites fail to lay eggs. In contrast, the offspring from gravid females collected at the same time as the long-distance migrants were moving southward, continue to lay eggs throughout the winter months. Or, if females are collected during the early summer and mid-summer period, eggs will be laid and the offspring continue to do so throughout the winter months (Urquhart and Stegner op. cit.).

Of those that migrate over short distances, as in the case under consideration, there is no ovarian dormancy and they do not cluster on roosting sites. However, as indicated in this study, the movements do coincide in time with those of the longdistance migrants of the Eastern North American Population eg. a northeasterly trend in the spring and early summer and a southerly trend in the late summer and fall.

One can hypothesize a definite advantage to an ovarian dormancy for long-distant flights. There would be less delay caused by oviposition. There would be less weight due to the absence of eggs. There would be more body fat available for longer flights. There would be a longer life period, extending up to six months (September to March) — gravid females on depositing their full complement of eggs live a much shorter time and it has been observed in our laboratory colonies that once oviposition starts, the appendages become brittle resulting in the loss of tarsi with the resulting destruction of the chemoreceptors and hence the inability of the individual to locate the source of food or indeed to be stimulated to oviposit; this process and the relationship between the chemoreceptor mechanism and food selection is now being investigated in our laboratory.

Ovarian dormancy occurs in over-wintering populations in northern California and in all of the other states of the United States and provinces of Canada with the exception of resident populations in southern California and southern Florida. It is interesting to note that all of North America, with the exception of southern Florida and southern California, has diurnal temperature fluctuations that repeatedly reach freezing or nearfreezing conditions from November through April with marked fluctuations in late September and October. This variation in diurnal temperatures can be correlated with the passage of cold fronts as a result of polar air mass outbreaks from the northwest (Urquhart op. cit.). Cold fronts rarely affect southern California and hence freezing temperatures are not frequently experienced there. A few examples of average monthly variations for Los Angeles are as follows: September 75° -59° F.; October, 72° - 55° F.; January and February, 63° - 43° F. A similar situation, with a tendency to higher maxima, occurs in Florida.

From the above it would appear that ovarian dormancy is correlated with marked fluctuations in diurnal temperatures in which the lows repeatedly reach freezing or near-freezing conditions. Such fluctuations are effective in the larval stage producing an ovarian dormancy in the adult females. In the absence of such marked fluctuations ovarian dormancy does not occur and breeding becomes continuous, assuming the presence of the host plant. This proposal would also explain the reason why no ovarian dormancy is experienced in the laboratory where temperatures are fairly constant thoughout the year (72° F.). Similarly, ovarian dormancy was absent in specimens reared in the greenhouse where light period was the same as that out-of-doors.

It has been noted that the population under consideration exhibits movement to the southeast and southwest with a few direct southerly flights. This peculiarity fits the same pattern applicable to the Eastern Populaion (Urquhart op. cit.). To account for this tendency, one may propose the following explanation: That a positive phototaxic response would account for the southeasterly movement in the a.m. period and southwesterly movement in the p.m. period with only a slight south movement during the short meridian period. This conception is indicated in laboratory observatons in which butterflies congregate at the section of the cage where the light is most intense; thus in the a.m. period they congregate in the southeast section and in the p.m. period in the southwest section.

It is probable that many species of insects that are not considered migrants, although sight observations would indicate movement, follow a pattern similar to that discussed in this study. Thus, movements tend to be directional at one time of the year and not at another, which may occur during the breeding season for those species which do not possess an ovarian dormancy period. By utilizing the marginal alar tag system for the larger species of Lepidoptera it might be found that those species which are suspected of being long-distant migrants follow a similar pattern. There are periodic migrations over long distances by various species of Lepidoptera in which one would suspect a similar pattern on a restricted basis during most years, but with a definite trend over long distances at other times. Our studies are now being expanded to include the movements of other species of Lepidoptera, employing the alar tag system.

SUMMARY

The marginal alar tag system for following the movements of individuals of a population was employed to find out whether or not members of a continuously breeding population showed a tendency to migrate. It was found that a restricted migration did take place and that the direction and time of movement followed the same sequence as the eastern North American population that has been shown to travel great distances. The continually breeding population was compared to one possessing an ovarian dormancy period. It was suggested that this dormancy period permitted longer flights because of increased longevity, time saved by not ovipositing, decreased weight and the availability of stored fatty material. A correlation between low temperature fluctuations in late summer and fall and ovarian dormancy was indicated. It is suggested that perhaps other species of insects follow a similar flight pattern to that discussed in the present study and that in so far as the larger species of Lepidoptera are concerned, the use of the marginal alar tag system might give definitive data upon which an accurate analysis could be made rather than an analysis based on slight records. It is further suggested that, although movement on the part of a species may be over a short distance the number of individuals taking part may vary with seasonal changes, particularly in the case of unusually long periodic flights.

ACKNOWLEDGMENTS

We are indebted to Mr. J. T. Carlisle of Whittier, California who was responsible for rearing, tagging and reporting on a large percentage of the population studied.

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